Habitat, Food and Reproductive Activity
of the Nudibranch *Hexabranchus sanguineus*
on Tongatapu Island

BY

MALCOLM P. FRANCIS [1]

'Atenisi Institute, Nuku'alofa, Tonga

(4 Text figures)

INTRODUCTION

THE TAXONOMY OF THE GENUS *Hexabranchus* Ehrenberg, 1831 is confused and requires revision. More than 20 species have been described (see THOMPSON, 1972), many of them based primarily on differences in colour pattern. Some authors (BERGH, 1900; ELIOT, 1904; THOMPSON, 1972) consider the many named species to be merely colour varieties of *Hexabranchus sanguineus* (Rüppell & Leuckart, 1828). The validity of the use of colour pattern as a taxonomic character remains to be demonstrated in this genus. Nevertheless, a full description of the colour pattern of Tongan *Hexabranchus* is given below to facilitate comparative studies in the event that colour does prove to be distinctive. External and internal morphology appear to vary little among the described varieties (ELIOT, 1904) but these features were not investigated in Tongan animals.

In the absence of any distinctive taxonomic characters, Tongan *Hexabranchus* are here referred to the type species of the genus, *H. sanguineus* (Rüppell & Leuckart). Other described "species" will here be considered simply as colour variations of *H. sanguineus*.

Little work has been done on the biology or ecology of *Hexabranchus*. The only comprehensive study is that of GOHAR & SOLIMAN (1963) on Red Sea specimens. Several authors have commented on feeding and stomach contents, and a review of their results is presented below. OSTERGAARD (1950) has described spawning and development in 2 Hawaiian varieties.

The only *Hexabranchus* previously recorded from Tonga is *H. flammulatus* (Quoy & Gaimard, 1832). Specimens 10 to 13 cm long were collected during the voyage of the *Astrolabe* from Tongatapu Island (21°10'S; 175° 10'W; see Figure 1).

DESCRIPTION

The colour of the dorsum and foot of *Hexabranchus sanguineus* varied from pale pink to dark red. The general appearance was, however, influenced by the colour, size
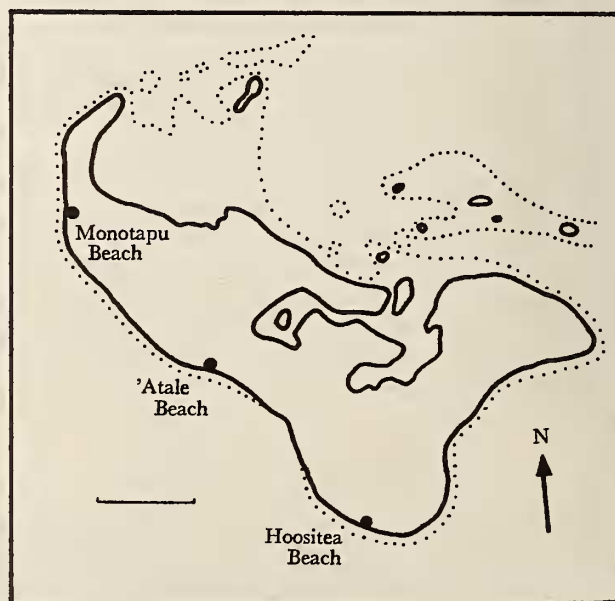

Figure 1

Tongatapu Island, Tonga, showing localities mentioned in the text. Dotted line indicates the edge of the fringing reef. Scale=5 km

---

[1] Present address: 44 Belmont Terrace, Auckland 10, New Zealand

and density of spots covering the dorsum; these ranged from large dense yellow spots (producing an overall orange appearance) to small white spots (which allowed the background colour to dominate the appearance). Most of the animals seen were dark red with these dense yellow spots on the dorsum (Figure 2, zone A).
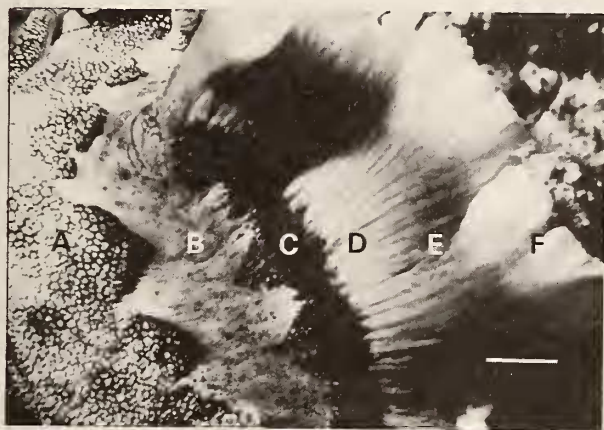

Figure 2

Close-up photograph of a large *Hexabranchus sanguineus* showing colour zones. See text for explanation of colour pattern of the various zones. Scale = 1 cm

In animals longer than about 6 cm, 5 colour bands were distinguishable on the notum (see Figure 2). Band B was comprised of a translucent layer of white pigment overlying dark red tissue, producing an overall mottled pink band punctuated with red spots. Band C was a dark red colour. Occasionally, band B was interrupted by a dark red intrusion from band C which linked with the dorsum. These intrusions probably represent areas from which the overlying pigment of band B is absent.

Band D was white with dark red lines radiating out from band C. These lines merged to produce a mauve coloured band E. The edge of the notum, band F, was always white.

Animals shorter than 6 cm were very similar to larger animals, except that bands D and E were frequently merged to form a single light purple band.

One small animal (1.8 cm long) had a different colour pattern. The notum had only 3 colour bands: a white margin tinged with blue, a central orange band with violet notches along its distal edge, and an inner white band. This could represent the juvenile colour pattern,

with the number of bands increasing with animal size as the violet notches coalesce to produce the characteristic red and purple bands of all larger animals.

The underside of the notum and the foot were dark red with yellow or white spots.

The rhinophores were red, and spotted with yellow or white, and the lamellae were red with yellow edges. The rhinophore collars were densely spotted with yellow or white and had bright red rings around their distal edges.

The gills were yellow and veined with red.

The only significant difference in colour pattern between Tongan *Hexabranchus* examined in this study and *H. flammulatus* described by Quoy & Gaimard (1832: plt. 17, figs. 6 & 7) is the presence in the latter of distinct white pennants punctuated with red adjoining the dorsum. These pennants clearly represent the remains of colour band B after it has been split into segments by dark red intrusions from band C. Distinct segments were not observed in the present study and band B was usually continuous around the whole notum. Distinct segments appear to be a feature of Australian *Hexabranchus* and are clearly seen in illustrations by Gillett & McNeill (1959: plt. 84) and Thompson (1972: fig. 2B). Otherwise, Tongan and Australian animals differ little in colour pattern.

Hexabranchus marginatus (Quoy & Gaimard, 1832) as illustrated by Bergh (1905: plt. 1, fig. 2) has an almost continuous band B and is very similar to Tongan animals. The only visible difference is that band D in *H. marginatus* is yellow in Bergh's figure, although Quoy & Gaimard's original description (1832: 255) gives it as white.

METHODS

During a preliminary survey of the coastline of Tongatapu Island, *Hexabranchus sanguineus* were found to occur predominantly on the shallow fringing reef platforms all around the island except on the sheltered north coast. The animals were most common on the south and southwest coasts where the fringing reef is approximately 100 m wide. Two sections of reef, at Hoositea Beach and Monotapu Beach (Figure 1), were chosen for further study and were visited regularly between March and November 1976.

HOOSITEA BEACH

A section of reef 100 m long was searched from the beach to the reef rampart (a distance of 125 m) at ap-

proximately monthly intervals between March and October 1976. Searches were conducted at low tide and covered an area of 1.25 hectares. All *Hexabranchus sanguineus* found within the area were counted and measured to the nearest centimeter below extended crawling length (excluding the foot). This measurement corresponds with the standard mantle length, Am, of Risso-Dominguez (1963). Channels in the reef were examined by snorkel diving.

Sea surface temperatures were measured at mid-morning over the low tide period in surge channels just inside the edge of the reef.

Specimens of *Hexabranchus sanguineus* were collected, cleaned of adhering debris and placed individually in seawater-filled jars which were then submerged in reef channels. After 1 to 5 hours the animals were released and their faeces collected and preserved in neutral formalin.

MONOTAPU BEACH

The inner 85 m of a section of reef 60 m long was searched at least once a month from April to November 1976. Searches were conducted at low tide and covered an area of 0.5 hectare. The outer edge of the reef was not searched because preliminary surveys had shown *Hexabranchus sanguineus* to be absent from this part of the reef, where a strong current flowed across the reef from the south.

All *Hexabranchus sanguineus* egg coils found within the area were counted and removed (to ensure that no egg coil was counted in a subsequent search).

Faecal samples were collected from live animals as for Hoositea Beach.

RESULTS

HABITAT

Hexabranchus sanguineus were abundant on shallow reef platforms on exposed coasts. In one 3-hour period, 45 animals were found in the 1.25 hectare area searched at Hoositea. *Hexabranchus sanguineus* could only be found readily over the low tide period. At other times they disappeared from view, probably into coral crevices in the reef.

Reef platforms on exposed Tongan coasts are protected from the prevailing south-easterly swells by raised ramparts at their seaward edges. The extent of protection afforded to reef platform organisms depends upon the state of the tide: during the low tide the water remaining on the reef is calm, whereas at high tide waves break over the rampart producing turbulent conditions.

The rampart at Hoositea shelters the reef for about half of the 12-hour tidal cycle. The reef is almost horizontal in profile and is covered by about 1.5 m of water at high tide. At low tide the reef dries almost completely, except for the numerous channels in the reef. These channels are up to 2 m deep and run at right angles to the beach.

Monotapu has a similar reef structure to Hoositea, but the reef is subject to turbulent wave action for about $\frac{2}{3}$ of the tidal cycle, and does not drain completely at low tide. A layer of water 10 cm to 30 cm deep remains at low tide.

The reef platform around most of Tongatapu Island is composed of compacted fused coral, and covered by a turf of coralline algae. Live coral (mainly *Porites* and *Acropora* species) is rare and confined to the channels which are water-filled at all times. Patches of dead *Acropora* project up to 30 cm above the level of the reef flat.

At low tide, *Hexabranchus sanguineus* were usually found crawling over the substrate, either among dead *Acropora* branches or on the algal turf. The animals actively avoided live coral, but were frequently seen moving among the algae-encrusted bases of live coral. They were rarely found in the reef channels, but sometimes occurred on the vertical sides of the channels.

Hexabranchus sanguineus probably shelter in coral crevices over high tide and thus reduce the risk of being swept from the reef or being damaged by the abrasive action of suspended sediment.

The distribution of *Hexabranchus sanguineus* across the reef was found to be non-random with respect to the size of the animal. The distribution by size was analysed during one low tide sampling period (1 July 1976), and the results are presented in Figure 3. Animals less than 3 cm long occurred only on the outer edge of the reef near the rampart. *Hexabranchus sanguineus* between 3 cm and 7 cm were found throughout the outer half of the reef, and large animals (exceeding 7 cm) occurred over the whole reef, but were most common on the inner half.

WATER TEMPERATURE

At Hoositea, water covering the outer $\frac{1}{4}$ of the reef platform is continually renewed at all tides by the influx of ocean water through the surge channels in the reef rampart. The outer section of the reef platform is therefore buffered against large diurnal fluctuations in temperature and salinity. The inner $\frac{3}{4}$ of the reef is more subject to temperature changes due to solar heating and
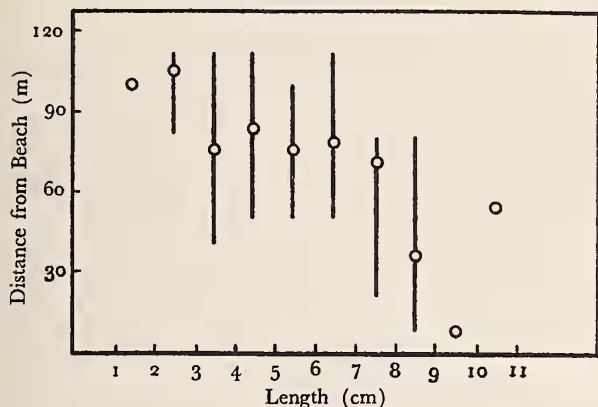
Figure 3

Distribution of *Hexabranchus sanguineus* across Hoositea reef by size (n=45). Open circles indicate mean distance of each size class from the beach, and vertical lines indicate the observed ranges. Size classes with no marked range were represented in the sample by only one specimen each

Figure 4

Number of egg coils of *Hexabranchus sanguineus* found at Monotapu (open circles) and sea surface temperature measured at Hoositea (closed circles)

night-time cooling, and salinity changes due to evaporation and freshwater seepage from the beach.

Temperature and salinity conditions at Monotapu are more constant than at Hoositea. The water level over the reef does not drop as low at Monotapu, and ocean water circulates continuously over most of the reef.

Sea surface temperatures measured at Hoositea are plotted in Figure 4, and indicate the trends during the period April to October. Temperatures ranged from 22.5° C to 27.6°C. The highest temperature recorded in the shallow water overlying the inner sections of Hoositea reef was 29.4°C; higher temperatures than this would be expected from January to March.

REPRODUCTIVE ACTIVITY

The egg coils of *Hexabranchus sanguineus* found in Tonga were consistent with the description of GOHAR & SOLIMAN (1963: 230 - 231). Freshly-laid coils were bright red, fading to a dull red-brown colour as the embryos developed.

The number of egg coils found at Monotapu fluctuated randomly from April to November (Figure 4). Egg coils were found in varying numbers during the coldest months, but apparently disappeared as the water temperature started increasing again. The absence of samples from the hottest part of the year precludes a full comparison of reproductive activity with seawater temperature.
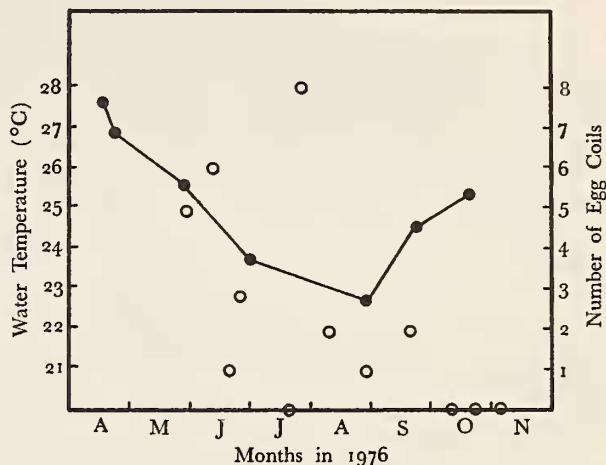
Hoositea was less preferred as a breeding site than Monotapu. Only 2 egg coils were found at Hoositea despite the much larger area searched throughout the study period.

SIZE STRUCTURE OF THE HOOSITEA
POPULATION

The size-frequency distributions of the Hoositea *Hexabranchus sanguineus* samples are shown in Table 1. Very small individuals were probably present throughout the study period, despite their absence from the first 2 samples. An animal 1.8 cm long was found at 'Atele Beach (Figure 1) on 19 April 1976, and a 1.5 cm animal (the smallest found in this study) at Hoositea on 24 April 1976. Even the 1.5 cm long animal was able to flare its notum when disturbed, and was able to swim. Large adults were present throughout the study, although none larger than 14 cm was found.

Most of the large samples had unimodal size-frequency distributions with modes between 5 cm and 7 cm. Small size classes have probably been under-represented because of their cryptic coloration. Since animals less than 4 cm were present from April to October, it appears that larval settlement on the reef occurs throughout this period. Larval settlement was especially heavy some time prior to the sample of 29 May 1976, as this sample contained

Table 1

Size-frequency distribution of samples of *Hexabranchus sanguineus* taken at Hoositea Beach.

Date of sample in 1976	Length (nearest cm below)													Number in sample
	1	2	3	4	5	6	7	8	9	10	11	12	13	
14 March					1		3	2		1	1	2		10
18 April			1	1	2	3	1	1	1		3	1	2	16
29 May	2	3	1	1	4	5	2	4	4	2	1	1		30
1 July	1	5	5	5	7	9	7	4	1	1				45
30 July			3	6	8	5	6	1	1		1			31
30 August		2	2	4	8	9	7	6	3		1		1	43
26 September			2	2	4	2	1	3	2	3	2	1	1	23
22 October			1	2	3	4	7	5	1	2	1		1	27

many small animals. The strong size class could also be detected in subsequent samples.

Few animals longer than 10 cm were found.

FEEDING

An examination of faecal material showed that *Hexabranchus sanguineus* feeds on sponges. All of the 13 faecal samples collected contained a large proportion by volume of sponge spicules. The species eaten, based upon spicule identification of 6 faecal samples, are shown in Table 2. *Hexabranchus sanguineus* feeds on at least 11 genera of sponges from 5 orders and 2 classes, and is clearly a non-selective browser.

A wide variety of non-sponge material was also identified from the faeces. Non-sponge components of the gut contents found in this study and by other authors are listed in Table 3. This material never formed more than a small proportion of the faecal material of Tongan animals.

Table 2

Sponge species identified from faeces of *Hexabranchus sanguineus* and their frequency of occurrence.

Sponge species	Number of animals in which sponge was found (n = 6)
CALCAREA	
Calcareous triradiates	2
DEMOSPONGIAE	
CHORISTIDA	
Stelletta sp.	1
Ancorina acervus (Bowerbank)	1
Pachastrella sp.	1
HADROMERIDA	
Cliona sp.	3
HAPLOSCLERIDA	
Haliclona sp. or *Adocia* sp.	2
Callyspongia sp.	3
POECILOSCLERIDA	
Xestospongia exigua (Kirkpatrick)	1
Petrosia sp.	5
Paraesperella sp.	1
Mycale sp. or *Zygomycale* sp.	4

Table 3

Non-sponge material identified from faeces of *Hexabranchus sanguineus*.

Material	Source
Algae	ABOUL-ELA (1959); GOHAR & SOLIMAN (1963); present study
Foraminifera	EALES (1938); GOHAR & SOLIMAN (1963); present study
Hydroids	BERGH (1900); ELIOT (1906)
Alcyonarians	GOHAR & SOLIMAN (1963)
Coral fragments	GOHAR & SOLIMAN (1963); present study
Worm tubes	BERGH (1900); EALES (1938); present study
Gastropod shells	EALES (1938); present study
Amphipods	Present study
Crab chela	Present study
Polyzoans	ELIOT (1906)
Echinoderm shells	EALES (1938)
Ascidian spicules	THOMPSON (1972)

DISCUSSION

REPRODUCTIVE ACTIVITY

Red Sea populations of *Hexabranchus* continued to breed throughout the year but activity declined during the cold months (GOHAR & SOLIMAN, 1963). The number of egg coils at Monotapu showed no relationship to seawater surface temperature during the 8 months of observations (Figure 4). GOHAR & SOLIMAN (1963: 242) believe that spawning in *H. sanguineus* is induced by increasing temperatures following winter low temperatures. The minimum temperatures in the Red Sea (16°C to 19° C [GOHAR & SOLIMAN, *loc. cit.*]) were considerably lower than the lowest temperature measured during the Tongan winter (22.5°C), and it is possible that the temperature of Tongan waters is suitable for uninterrupted year-round breeding.

The scarcity of egg coils at Hoositea was probably due to unfavourable environmental conditions. The temperature of water trapped in channels at low tide during the day increases and the dissolved oxygen concentration probably decreases. GOHAR & SOLIMAN (1963) observed retardation of embryo development in stagnant water. Egg coils kept in a non-circulating aquarium in this study disintegrated before larvae were ready to hatch. The continual renewal of seawater at Monotapu produces a more constant environment for larval development than exists at Hoositea.

FEEDING

Hexabranchus sanguineus is a sponge feeder, consuming a wide variety of species. The sponges taken are mainly inconspicuous encrusting species, probably occurring in crevices and holes in the reef matrix (P. Bergquist, personal communication). Most other workers have also recorded sponges in the diet of *Hexabranchus*. BERGH (1900: 231) found "fragments of transparent spicules" and "masses of simple and three-rayed silica needles" in one specimen; these were obviously sponge remains. ELIOT (1906) and GOHAR & SOLIMAN (1963) noted that sponges form at least part of the diet of *Hexabranchus*, and YOUNG (1966) reported the calcareous sponge *Leucetta solida* from the gut of a Hawaiian specimen. KAY & YOUNG (1969) concluded that 3 Hawaiian varieties of *Hexabranchus* were "rasping sponge feeders."

The wide variety of non-sponge material in the gut contents of the different varieties of *Hexabranchus* is indicative of an indiscriminate mode of feeding. The animals ingest much extraneous material while feeding on the encrusting sponges in the crevices where other organisms, animal skeletons and detritus also collect.

The contention that *Hexabranchus* is entirely herbivorous (ABOUL-ELA, 1959) is not supported. It is likely that algae are ingested accidentally during feeding, and they appear to pass through the gut undigested.

BLOOM (1976) has demonstrated a correlation between the radula and digestive morphology of dorid nudibranchs, and the type of sponge preferred as prey. Bloom's major thesis is that the presence of a gut caecum (a spicule-compacting organ) enables nudibranchs to handle large quantities of large sharp spicules, and they are therefore adapted to feeding on sponges with unorganised or non-reticulated skeletons. Conversely, nudibranchs lacking a gut caecum, but possessing a robust radula, are able to feed on, and digest, sponges with organised, reticulated skeletons. The only sponge prey of *Hexabranchus marginatus* mentioned by BLOOM (1976: table 3) is *Leucetta solida*, originally reported by YOUNG (1966). Thus, using limited data, Bloom finds that *Hexabranchus*, which possesses a caecum and radula teeth with a low degree of hook (Bloom's measure of tooth robustness) feeds on non-reticulated sponges; this supports his contention that a correlation exists between nudibranch morphology and sponge prey. However, the present study has shown that *H. sanguineus* consumes a wide variety of sponge types, ranging from unorganised non-reticulated sponges (calcareous species) to highly organised reticulated speces (*e. g.*, *Mycale* sp., *Petrosia* sp., *Callyspongia* sp.) (see BLOOM, 1976: table 1, for a description of skeletal structure in each of these groups). The presence of a gut caecum may indeed allow *Hexabranchus* to feed on non-reticulated sponges, but the absence of robust radula teeth does not prevent it from also eating reticulated sponges. Generalist sponge feeders are exceptions to Bloom's correlations, and other species may also prove to be generalists on closer study.

ACKNOWLEDGMENTS

Literature Cited

ABOUL-ELA, IBRAHIM AHMED
1959.   On the food of nudibranchs.   Biol. Bull. 117: 439-442

BERGH, RUDOLF LUDWIG SOPHUS
1900.   Die Opisthobranchier.   Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896-1897).   Zool. Jahrb. Syst. 13: 207-246; plts. 1-21
1905.   Die Opisthobranchiata der Siboga Expedition.   Siboga Exp. prt. 50: 1-248; plts. 1-20   (October 1905)

BLOOM, STEPHEN A.
1976.   Morphological correlations between dorid nudibranch predators and sponge prey.   The Veliger 18 (3): 289-301; 1 text fig.   (1 January 1976)

EALES, NELLIE B.
1938. A systematic and anatomical account of the Opisthobranchia. John Murray Expedition, 1933-34.   Sci. Reprt. Brit. Mus. (Nat. Hist.) 5: 77-122; 1 plt.; 28 text figs.

EHRENBERG, CHRISTIAN GOTTFRIED
1831.   Animalia evertebrata, exclusive insectis.   In: C. G. Ehrenberg & F. G. Hemprich (eds.), Symbolae physicae. Berlin

ELIOT, CHARLES NORTON EDGECOMBE
1904.   On some nudibranchs from East Africa and Zanzibar. Part 6. Proc. Zool. Soc. London 2 (I): 268-298; plts. 16, 17   (9 June 1904)
1906.   Nudibranchiata, with some remarks on the families and genera, and description of a new genus, Doridomorpha.   In: J. S. Gardiner (ed.), The fauna and geography of the Maldive and Laccadive Archipelagoes. 2: 540-573. Cambridge Univ. Press, London

GILLETT, KEITH & FRANK McNEILL
1959.   The Great Barrier Reef and adjacent isles.   Coral Press, Sydney. 194 pp.; 161 plts.; 3 text figs.

GOHAR, H. A. F. & GAMIL N. SOLIMAN
1963.   The biology and development of Hexabranchus sanguineus (Rüppell & Leuckart) (Gastropoda, Nudibranchiata).   Publ. Mar. Biol. Sta. Al-Ghardaqa 12: 219-247; 37 text figs.

KAY, ELIZABETH ALISON & DAVID KENNETH YOUNG
1969.   The Doridacea (Opisthobranchia; Mollusca) of the Hawaiian Islands.   Pacif. Sci. 23 (2): 172-231; 82 text figs. (30 April 1969)

OSTERGAARD, JENS MATHIAS
1950.   Spawning and development of some Hawaiian marine gastropods.   Pacif. Sci. 4: 75-115; 42 text figs.   (28 April 1950)

QUOY, JEAN RENÉ CONSTANT & JOSEPH PAUL GAIMARD
1832.   Voyage de découvertes de l'Astrolabe.   Zoologie, Mollusca 2. Tastu, Paris

RISSO-DOMINGUEZ, CARLOS J.
1963.   Measuring nudibranchs: a standardization for descriptive purposes.   Proc. Malacol. Soc. London 35: 193-202; 2 text figs.

RÜPPELL, WILHELM PETER EDUARD S. & FRIEDRICH SIGISMUND LEUCKART
1828.   Neue wirbellose Thiere des Rothen Meers.   In: Eduard Rüppell, Atlas zu der Reise im nördlichen Afrika 5. pp. 1-47; plts. 1-12

THOMPSON, THOMAS EVERETT
1972.   Observations on Hexabranchus from the Australian Great Barrier Reef (Gastropoda : Opisthobranchia).   The Veliger 15 (1): 1-5; 2 text figs.   (1 July 1972)

YOUNG, DAVID KENNETH
1966.   Systematics, food and functional morphology of the feeding apparatus of some dorid nudibranchs.   Ph. D. dissertation, Univ. Hawaii, Honolulu